

FACTORS DETERMINING THE ESTABLISHMENT OF PLANT ZONATION IN A SOUTHERN CALIFORNIAN RIPARIAN WOODLAND

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ABSTRACT

This paper describes plant zonation in a southern California riparian woodland and identifies the factors responsible for the zonation. Of the 25 common trees and shrubs in the Tijuana River Valley, three were numerically dominant: *Baccharis salicifolia* (Ruiz & Pav.) Pers., *Salix lasiolepis* Benth., and *Salix gooddingii* C. R. Ball, here referred to as BASA, SALA, and SAGO, respectively. Adults of these species displayed significant down-slope zonation, with BASA, SALA, and SAGO most abundant in the High, Intermediate, and Low zone, respectively. Among new recruits, SALA and SAGO seedlings displayed zonation similar to that of adults, indicating that the zonation of SALA and SAGO was established at the time of recruitment. In contrast, BASA seedlings were more broadly distributed than adults; they were abundant in all zones, particularly the Low zone where adults were rare, indicating that the zonation of BASA adults was established post recruitment. For SALA and SAGO, the timing of fruiting and timing of water-level decline were the factors producing adult zonation; the two species had nearly non-overlapping periods of seed production, and this led to zonation of their seedlings on the banks as water levels declined. The seedling zonation was then retained in the adults. Because factors affecting recruitment played an important role in their zonation, these two willow species provide a new example of the supply-side influencing community structure. For BASA, whose seedlings were widely distributed, zonation of adults was the result of poor seedling survivorship in the Low zone during the first winter and poor adult survivorship in the Intermediate zone later. Results of this study can help guide future riparian restoration projects in southern California. Based on the prolific natural recruitment and rapid development of dense, native-dominated stands, use of a natural restoration approach where possible is recommended instead of the more common horticultural approach.

Key Words: *Baccharis salicifolia*, fruiting phenology, riparian woodland, *Salix gooddingii*, *Salix lasiolepis*, recruitment, supply-side ecology, zonation.

Riparian habitats are rare in southern California because many of the rivers have been channelized, and there has been extensive development on the floodplains. An estimated 95% of the original riparian community has been eliminated during the past 200 years (Faber et al. 1989). Only recently has the value of these communities been recognized; remnant riparian habitats are now being preserved and protected, and each year a considerable amount of funding is directed towards their restoration and enhancement. Because these remnant riparian communities have not been well studied (Faber et al. 1989), and because there is little local information, project managers have to rely for guidance on studies conducted outside southern California where different species dominate, e.g., the desert Southwest (e.g., Stromberg et al. 1996), the Sierra Nevada (e.g., McBride and Strahan 1984a, b), and elsewhere (e.g., Krasny et al. 1988; Niiyama 1990; Mahoney and Rood 1998).

Many wetland plant communities are characterized by striking species-zonation patterns across elevational gradients (Keddy 2010). The study of these zonation patterns and the processes producing them have often led to a deep understanding of the entire community, e.g., algal

communities (Dayton 1971; Robles and Deshar-nais 2002), mangroves (Rabinowitz 1978; Sousa et al. 2007), and salt marshes (Pennings and Callaway 1992; Pennings and Bertness 2001; Pennings et al. 2005). There have been only a few studies of riparian community composition in southern California (Bendix 1994, 1999; Oneal and Rotenberry 2008), and none has examined zonation. A productive approach for determining the underlying causes of species distributions in general, and zonation in particular, is to examine the two “sides” of community development—the supply side and the interaction side (e.g., Lewin 1986; Roughgarden et al. 1987; Underwood and Fairweather 1989; Grosberg and Levitan 1992; Schmitt and Holbrook 1999). Supply side refers to factors such as seed production and dispersal that affect the supply of propagules to an area, and the interaction side refers to factors such as competition and predation that affect the survivorship of recruits in the community (Roughgarden 2009). The approach, therefore, is to determine when the zonation pattern becomes established, and this requires the study of reproduction, seedling establishment, and community development.

The most common perennial species in the riparian communities of southern California—*Salix* L. spp. (willows), *Populus* L. spp. (cottonwoods) and *Baccharis salicifolia* (Ruiz & Pav.) Pers. (mule fat)—reproduce in similar ways. They produce tiny, wind-dispersed seeds that are short-lived (Stella et al. 2006), have no dormancy requirement (Emery 1988), and germinate within hours of landing (Karrenberg et al. 2002, Boland unpublished data) in their recruitment safe sites (Harper 1977). These safe sites are places suitable for germination where the substrate is both moist and in the sun (Karrenberg et al. 2002; Seiwa et al. 2008), and they typically occur in a narrow band immediately above the water's edge, referred to as the capillary fringe (Mahoney and Rood 1998). The common species disperse seeds in phase with the seasonal retreat of floodwaters during spring and summer. Community development is rapid once seedlings are established (Faber et al. 1989) because members of the Salicaceae, willows in particular, are among the fastest-growing tree species (Karrenberg et al. 2002).

This study describes zonation in a southern California riparian woodland and identifies the factors that produce the zonation. In particular, this paper: (1) describes the distribution of adults within the community; (2) describes the distribution of seedlings in areas of new recruitment; (3) examines factors affecting recruitment—timing of fruiting, timing of water-level decline, and timing of seedling establishment—to determine their influence on adult zonation; (4) examines seedling survivorship and change in community structure over time to determine the influence of these post-recruitment factors on adult zonation; and (5) discusses how the findings can improve restoration projects. This study of patterns and processes in a riparian woodland is one of very few that simultaneously quantifies seed production, recruitment, and survivorship of co-occurring tree species.

STUDY SITE AND DOMINANT SPECIES

The Tijuana River Valley (32°33.080'N, 117°4.971'W) in San Diego Co., California, is a coastal floodplain that covers 1457 ha at approximately sea-level at the end of a 448,000 ha watershed. The climate is Mediterranean, with most of the rain falling between November and April (Zedler et al. 1992). The Tijuana River is an intermittent stream; flows are strong during winter and spring but cease during summer, reducing the river to a few widely-spaced pools. The river was confined to a narrow, unarmored channel during the 20th century when the valley was used extensively for agriculture, and riparian forests were absent (Boland, personal observation). Widespread flooding, particularly during

the 1980s, expanded the channel and forced out much of the agriculture (Zedler et al. 1992). The largest flooding events occurred in 1980, 1993, and 2005, and the riparian woodlands that developed in the flooded sites were therefore 32, 19, and 7 years old, respectively, in 2012. The riparian woodlands in the valley are still considered pioneer, because succession is slow in these communities and may take 50–70 or more years to complete (Faber et al. 1989). The woodlands are preserved within three adjoining parks: the County of San Diego's Tijuana River Valley Regional Park, the Border Field State Park, and the U.S. Fish and Wildlife Service's Tijuana Slough National Wildlife Refuge. They are relatively undisturbed and support numerous bird species, including the endangered *Vireo bellii pusillus* (least Bell's vireo) and *Empidonax traillii extimus* (southwestern willow flycatcher; U.S. Fish and Wildlife Service 1994, 2005). The riparian woodlands in the valley have not been studied previously, but the spread and dispersal of *Arundo donax* L., a non-native, invasive species, has received attention (Boland 2006, 2008).

The three most abundant species in the riparian habitats of the Tijuana River Valley are *Baccharis salicifolia* (Ruiz & Pav.) Pers., *Salix lasiolepis* Benth. (arroyo willow), and *Salix gooddingii* C. R. Ball (Goodding's black willow), here referred to as BASA, SALA, and SAGO, respectively. These dioecious species are common throughout California and the Southwest (Baldwin et al. 2012).

METHODS

Distribution of Adults

Riparian woodland bisect. To illustrate the down-slope characteristics of the vegetation, a bisect (*sensu* Barbour et al. 1987) was made through a 19-year-old woodland in the center of the valley (Fig. 1). A transect line was laid perpendicular to the course of the river from the highest riparian shrub on the floodplain to the center of the river (120 m). Every perennial tree and shrub within a 5 m belt alongside the line was identified and measured so that a scale drawing could be made. In addition, percent canopy cover of each perennial species was estimated within a 10 m-wide belt transect alongside the line (within 10 × 10 m quadrats). Ground elevations along the transect were measured with a GPS unit (Trimble R8 Model 2 GNSS rover), using the water level in the nearest pool in the river bed as the zero datum. GPS data were post-processed using Trimble Geomatics Office and Trimble Business Center.

Density. To document species composition and density within the riparian woodlands (19–

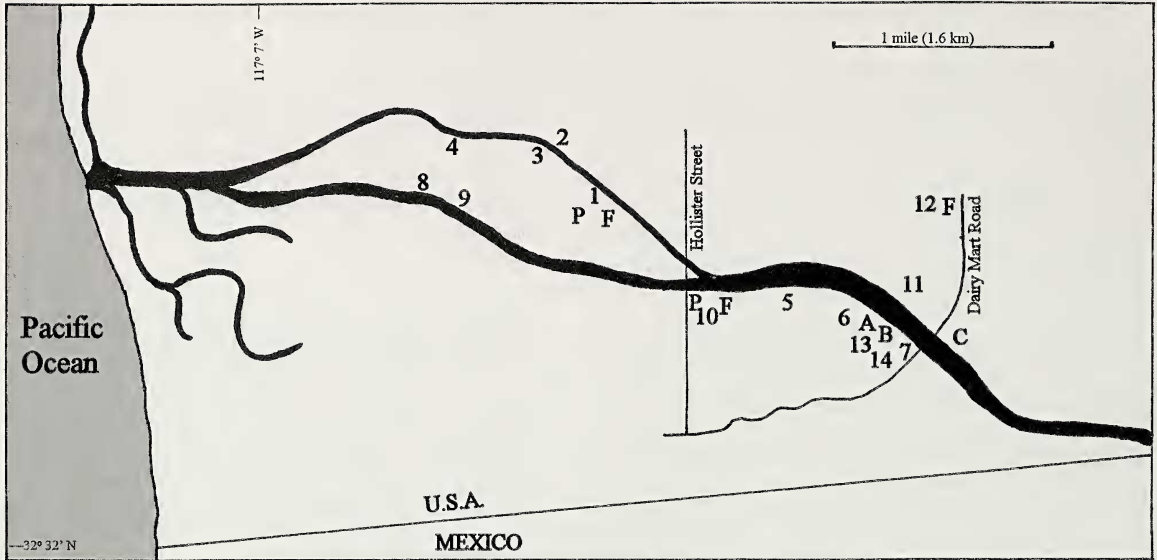


FIG. 1. Location of study sites in the Tijuana River Valley. Sites were used for the woodland bisect (1), density and relative abundance of adults (1–12), seedling profile (A), seedling density and survivorship (A–C), recruitment pots (two P), fruiting phenology (three F), woodland development (A–C, 1–4, 13–14), and BASA skeletons (1–4).

32 years old), quadrat surveys were conducted at 12 sites chosen in a stratified-random manner (Fig. 1). At each site, the habitat was divided into three zones — High (outside the forest), Intermediate (the forest edge), and Low (inside the forest) — and a 10×10 m quadrat was randomly placed in each zone. In each quadrat, all perennial trees and shrubs over 2 m tall were identified and counted. For each zone, density of each species was calculated as the mean number of individuals per 100 m² quadrat ($n = 12$).

Relative abundance. A second set of surveys was conducted at the same 12 sites to calculate the relative abundance of species and to test the distributions of BASA, SALA, and SAGO. [Statistical tests could not be done on the quadrat-survey results because the number of individuals in each quadrat was low.] A line transect was started at the location of the quadrat in the above density survey and run parallel to the course of the river within each zone. Along each transect, the first 33 perennial tree and shrub individuals over 2 m tall were identified and counted. Transect lengths varied with plant density and were 50–400 m long. This method used a similar sampling effort in each zone to collect a large, representative sample. Colonial plants, such as *Salix exigua* Nutt. (narrow-leaved willow), were counted as one individual if they intersected <10 m of the transect, or as two individuals if they intersected 10–20 m. [None intersected >20 m.] For each zone, the relative abundance of each species was calculated as the percent of the total 396 individuals censused in the zone. For BASA, SALA, and SAGO,

numbers of individuals in the three zones were compared using replicated G-tests of independence (Sokal and Rohlf 1995). Overlaps in the zonation of the species were calculated using the proportional similarity index (PSI) applied to the frequency distributions: $PSI = \sum \min(p_i, q_i)$, where p_i and q_i represent the proportion of species p and q in zone i (Zaret and Smith 1984).

The above adult surveys quantified the distribution and abundances of all the perennial species; the other aspects of this paper focus on only the three dominant species: BASA, SALA, and SAGO.

Distribution of Seedlings

Recruitment sites. Three recruitment sites (also called nursery sites, e.g., Mahoney and Rood 1998) were found in the Tijuana River Valley in December 2009 and followed during 2010. All three had been recently cleared of vegetation, were large enough to include the full range of floodwater elevations, were inundated during floods, and were within 200 m of adult riparian vegetation. The sites were named New Channel (650 m²), Dirt Road (780 m²), and Dairy Mart (1849 m²; Fig. 1). New Channel was a natural, freshly-scoured meander channel, whereas the other two sites had been cleared by bulldozers. Each site was visited regularly during early 2010 to monitor water levels and to stake the lowering water's edge. Each site was divided into three zones based on the water levels on particular dates. The division between the High and Intermediate zones was the water level in late February, the division between the Intermediate

and Low zones was the water level in late April, and the lower extent of the Low zone was the water level in mid-July. These dates were used because they corresponded to the fruiting periods of SALA and SAGO, which were being followed simultaneously as described below. Elevations of the zones were measured during summer with the GPS unit described above, using the water level in the nearest pool in the river bed as the zero datum. At the three sites, the High, Intermediate, and Low zones had mean elevation spans of: 0.66 (± 0.08 SD) m, 0.50 (± 0.02 SD) m, and 0.24 (± 0.07 SD) m, respectively, for a total elevation range of 1.4 m.

Seedling profile. To illustrate the down-slope distribution of the seedlings, a profile of the seedlings was made on a steep bank at New Channel during June 2010. A 6 m transect was laid perpendicular to the course of the river from the highest reach of the flood flows to the center of the river meander. BASA, SALA, and SAGO seedlings were identified to species, and their densities were measured within quadrats (20×20 cm) at 0.5 m intervals along the transect.

Seedling density. To document the distribution and density of seedlings at the three recruitment sites, seedlings were censused soon after they grew their first few leaves and could be identified to species. Because recruitment occurred first in the High and Intermediate zones as the water level declined, these zones were censused first (April to July 2010). The Low zones were censused later (June to July 2010). At each site, 1–3 transects were randomly placed within each zone parallel to the course of the river along elevation contours, and BASA, SALA, and SAGO seedlings were counted within quadrats (20×20 cm) at 1 m intervals along the transect. A total of 261 quadrats (86, 87, and 88 at the three sites) and 9040 seedlings were counted. For the purpose of this paper, the term recruits refers to these new seedlings (<5 months old). Overlaps in the zonation of the species were calculated using the PSI as above (Zaret and Smith 1984), and distributions of the species were tested using replicated G-tests of independence (Sokal and Rohlf 1995).

Factors Affecting Recruitment

Fruiting phenology. To determine temporal changes in seed production, fruiting of the three species was monitored weekly from December 29, 2009 through August 4, 2010 ($n = 32$ wk). Each week the same 12–15 adult females of each species were visited in three areas of the valley (Fig. 1). These plants had mean heights (\pm SD) of: 10.3 (± 3.0) m for SAGO ($n = 15$); 6.5 (± 1.3) m for SALA ($n = 12$); and 2.9 (± 0.2) m for BASA ($n = 12$). Fruiting flowers (BASA) and

fruiting catkins (SALA and SAGO) have a conspicuous fluffy appearance and, using the naked eye and binoculars, their percent cover on each plant was estimated from within 15 m of the plant. For consistency, the same person collected all of the fruiting data. Percent-cover data were arcsine transformed and averaged, giving the mean percent cover of fruiting flowers for each species on each survey date. Because the counts were of the mature, fluffy seeds that were ready for dispersal, the percent-cover data collected estimated both the abundance of fruiting and of seed production. Overlap between fruiting frequency distributions of the three species was calculated using the PSI as above (Zaret and Smith 1984). Similar visual estimations of percent cover are commonly used in field studies and have been shown to be accurate (e.g., Dethier et al. 1993; Bråkenhielm and Qinghong 1995). In this study, repeat estimates done on the same day indicated that the percent-cover method was sufficiently precise; the root mean square error of paired counts was $\pm 4\%$, which compares favorably with a different fruiting abundance method used by Stella et al. (2006), who found the root mean square error of their paired counts to be $\pm 10\%$.

Timing of recruitment. To examine temporal changes in recruitment, artificial safe sites were made available for short periods during the fruiting months. Simple seed traps could not be used because the seeds of SALA and SAGO cannot be distinguished (Boland personal observation). The artificial safe sites, or recruitment pots, were flower pots filled with moist sand. These provided suitable conditions for seeds that landed on them to germinate and grow to a size at which they could be identified to species. The pots were one-gallon, plastic flower pots (16.5 cm tall, 15 cm diameter, 0.018 m² surface area) filled with clean sediment from the nearby Goat Canyon sedimentation basin. This sediment has been identified as 53% sand, 40% clay, and 7% silt, and is classified as sandy clay (Nautilus Environmental, unpublished data). Each pot was placed alone in a plastic basin (14.2 liter; $35 \times 31 \times 15$ cm) that was filled with water so that the surface of the sediment in the pot was kept moist through capillary action.

Ten recruitment pots (with their basins) were put out each month from January to August 2010 ($n = 8$ monthly sets of pots). They were placed close to the river, 1 m apart, in two open areas within the riparian habitat; five pots were in the riparian forest near Hollister Bridge, and five were in the riparian shrub community approximately 800 m to the west (Fig. 1). The pots were left in the field for two weeks, during which time wind-borne seeds landed on the sediment surface,

germinated, and began to grow. After two weeks of exposure, the pots were taken to a sunny location outside the valley where they were kept moist in basins of water. The pots were covered with a fine netting to exclude any new seeds, and seedlings were grown to a size that allowed species identification, approximately 1 cm tall. Seedlings in each pot were counted after 4–10 wk (winter seedlings needed longer to grow than summer seedlings). Each month, one control pot was prepared and treated like the others, but was not exposed in the field. No seedlings grew in the control pots, showing that the sediment contained no viable seeds. For analysis, the five pots at each site were treated as subsamples, and the average number of seedlings per pot was calculated each month as the average of the two sites ($n = 2$ sites). For each species, the strength of the link between fruiting percent cover and the number of seedlings in the pots was quantified using linear regressions. Arcsine-transformed fruiting percent-cover data were averaged for the two-week period that the recruitment pots were in the field, and that average was run against the average number of seedlings per pot during the same period. Correlation coefficients were tested for significance using the t-test (Sokal and Rohlf 1995).

Water-level change and the predicted distribution of seedlings. To test whether only the timing of fruiting and the timing of water-level change could account for the observed zonation of seedlings, the two factors were combined into a Seedling Distribution Prediction Index (SDPI). Fruiting data for 2009–2010 were from the section above. Water-level data for 2009–2010 were obtained from the International Boundary and Water Commission for station #1000, which is on the Tijuana River approximately 2 km upstream from the study sites. Daily flows (cubic m per second) were converted to daily elevations (height in m above stage) using the rating table for the station. Precipitation data for the same period were obtained from the Tijuana River National Estuary Research Reserve's weather station, which is approximately 4 km downstream from the study sites. To determine the SDPI for each species, the total range of water levels during 2009–2010 was divided into 1 cm intervals, and the 1 cm intervals were populated with virtual seeds by putting the fruiting percent cover for each day ($n = 32$ d) into that day's water level. The virtual seeds were then summed for each 1 cm interval. The resulting SDPI for each species showed the predicted distribution of seedlings against height on the river bank, based on only fruiting and water levels. Overlaps in the zonation of species in the SDPIs were calculated using the PSI as above (Zaret and Smith 1984).

Post-recruitment Factors

Seedling survivorship. The 2010 seedling cohort was re-censused twice to determine survivorship over the first summer and the first winter. To measure survivorship over the first summer, seedlings at the three recruitment sites were re-censused in late summer (August to September 2010). The time between the initial census and this second census averaged 68 days (± 11.5 SD) for each zone at the three sites ($n = 9$). At each site, 1–3 horizontal transects were placed in each zone, and BASA, SALA, and SAGO seedlings were counted within quadrats (20×20 cm) at 1 m intervals along each transect. A total of 218 quadrats (86, 46, and 86 at the three sites) and 4279 seedlings were counted. Transects and quadrats were in approximately the same positions as those in the initial census described above.

To measure survivorship over the first winter, the seedlings (now yearlings) were censused again during summer 2011 (May to August). The time between the second (late summer) and this third census averaged 309 days (± 16.4 SD) for each zone at the three sites ($n = 9$). At each site, 1–3 horizontal transects were placed in each zone, and yearlings were counted within quadrats (20×20 cm) at 1 m intervals along each transect. Transects and quadrats were in approximately the same positions as those in the initial census. A total of 275 quadrats (90, 92, and 93 at the three sites) and 396 yearlings were counted. These yearlings (approximately 1.5 years old) were easily distinguished from any new 2011 recruits by their larger size; yearlings were ~ 1.5 m tall, whereas new recruits were ~ 5 cm tall.

Riparian woodland development. To understand changes in community structure during woodland development, four characteristics were measured within stands of different ages. The characteristics were plant density, canopy height, canopy percent cover, and light level. The stand ages were 0.5 years ($n = 3$); 1.5 years ($n = 3$); 7 years ($n = 2$); and 19 years ($n = 4$; Fig. 1). **Plant densities** of BASA, SALA, and SAGO were obtained from the seedling, yearling, and adult surveys described above. Additional densities were obtained in two 7-year-old stands. In these stands, 1×1 m quadrats were placed at 3 m intervals along 30 m transects parallel to the river flow ($n = 11$ quadrats in each zone at each site). **Maximum canopy heights** were measured with a meter stick, stiff meter tape, or laser distance measurer (Bosch DLR130K). In the 0.5- and 1.5-year-old stands, heights were taken every meter along transects parallel to the river flow ($n = 18$ –32 measurements in each zone at each site). In the 7- and 19-year-old stands, heights were taken every 10 m along 30 m transects parallel to the river flow ($n = 3$ measurements in each zone at

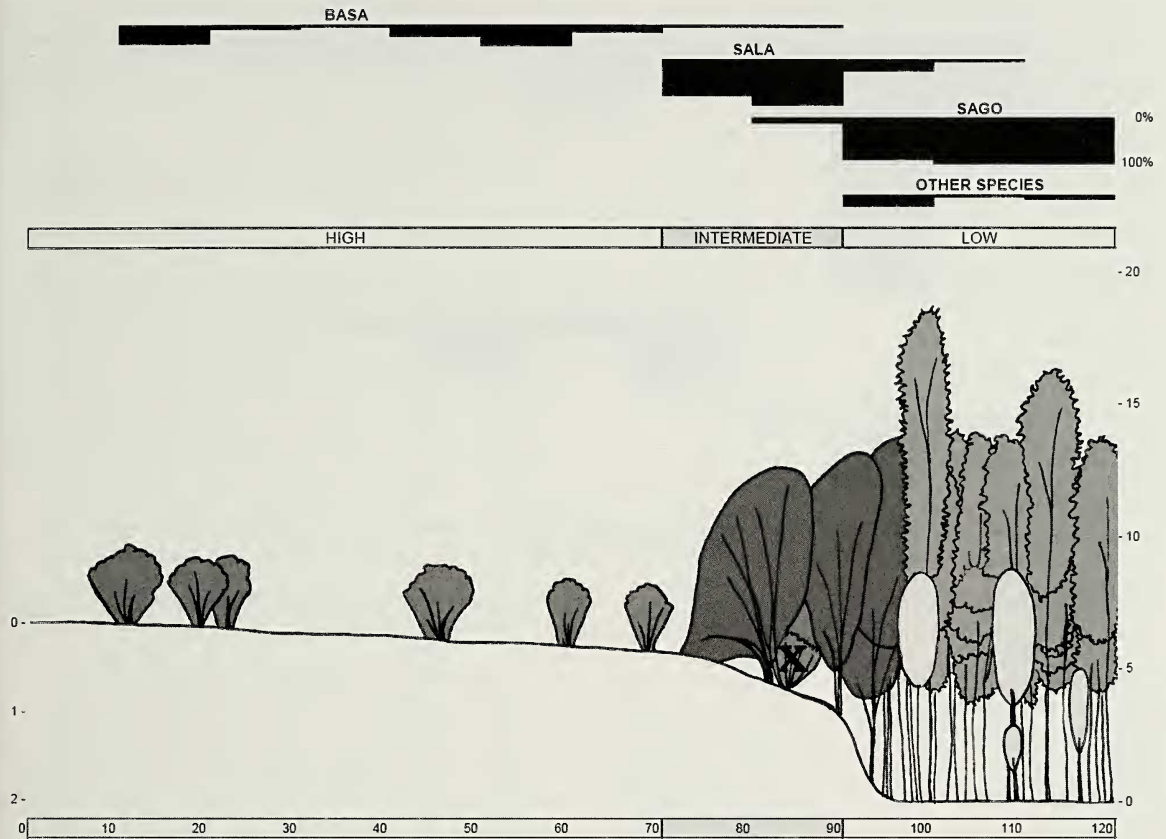


FIG. 2. A bisect through a typical 19-year-old riparian woodland in the Tijuana River Valley. The bisect ends in the center of the river bed, and the opposite bank is a mirror image of the one shown. Canopy percent cover is shown above. Scales for elevation (left), tree height (right), and distance (bottom) are in meters. The X indicates an adult BASA that was almost dead.

each site). **Percent canopy cover** measurements were taken 1.15 m above ground level using a spherical densiometer (Forest Densimeters). At all sites, measurements were taken at 3 m intervals along 30 m transects parallel to the river flow ($n = 10$ measurements in each zone). **Light levels** were measured at 1.15 m above the ground, during midday (11:30 a.m.–1:30 p.m.) on cloudless days using a light meter (Extech Instruments Model 401025). At each site, light was measured first outside the riparian zone in bright sunshine (ambient), then within each zone, and finally outside the riparian zone a second time. At all sites, measurements were taken at 3 m intervals along 30 m transects parallel to the river flow ($n = 10$ measurements in each zone). Light levels in each zone were averaged, and are presented as the percent of the ambient light level.

BASA skeletons. Because dead BASA were conspicuous in the Intermediate zones of the forests, the height of BASA skeletons and the canopy overhead were documented. At each of the four 19-year-old stands, a transect line was randomly placed parallel to the river in the

Intermediate zone. Of the first 50 BASA individuals along the transect (30–50 m in length), the tallest 10 BASA skeletons were flagged. The height of each flagged skeleton was recorded, along with the height of the willow canopy directly overhead at that spot.

RESULTS

Distribution of Adults

The bisect at one site showed that the riparian woodlands in the Tijuana River Valley consisted of a tall forest in the riverbed with shorter shrubs on the terraces above (Fig. 2). It also showed that three species—BASA, SALA, and SAGO—were dominant and exhibited a distinct down-slope zonation pattern. Each species had its greatest density and canopy cover in a different zone: BASA in the High zone on the upper terraces; SALA in the Intermediate zone at the edge of the forest; and SAGO in the Low zone within the forest in the riverbed.

The more extensive surveys of adults in the 19- to 32-year-old sites reinforced this view of a

TABLE 1. DENSITY AND RELATIVE ABUNDANCE OF THE PERENNIAL SPECIES WITHIN THE ADULT RIPARIAN WOODLANDS OF THE TIJUANA RIVER VALLEY. Density is the average number of individuals per quadrat (100 m²) within each zone (n = 12 sites). Relative abundance is the percent of total individuals along line transects (n = 396 individuals in each zone). Nomenclature follows *The Jepson Manual* (Baldwin et al. 2012). N = native; ex = non-native/exotic; INT. = Intermediate zone.

Species name	Common name	Origin	DENSITY			RELATIVE ABUNDANCE		
			HIGH	INT.	LOW	HIGH	INT.	LOW
<i>Baccharis salicifolia</i> (BASA)	Mule fat	N	3.0	0.6	0	68%	10%	3%
<i>Salix lasiolepis</i> (SALA)	Arroyo willow	N	0	3.4	1.3	3%	78%	15%
<i>Salix gooddingii</i> (SAGO)	Goodding's black willow	N	0	0.8	5.9	0.8%	8%	76%
<i>Salix exigua</i>	Narrow-leaved willow	N	0.3	0.7	0.1	9%	1%	0
<i>Ricinus communis</i>	Castor bean	ex	0.2	0.6	0.3	4%	1%	2%
<i>Baccharis sarothroides</i>	Broom baccharis	N	0.2	0	0	4%	0	0
<i>Myoporum laetum</i>	Myoporum	ex	0	0.1	0	2%	0.3%	0
<i>Arundo donax</i>	Giant reed	ex	0	0	0.1	2%	1%	2%
<i>Tamarix ramosissima</i>	Tamarisk	ex	0.1	0	0.3	1%	0	0.8%
<i>Isocoma menziesii</i>	Coastal goldenbush	N	0	0	0	1%	0	0
<i>Nicotiana glauca</i>	Tree tobacco	ex	0.3	0	0	1%	0	0
<i>Atriplex lentifolius</i>	Big saltbush	N	0	0	0	0.8%	0	0
<i>Hymenoclea monogyra</i>	Desert fragrance	N	0.4	0	0	0.8%	0	0
<i>Acacia cyclops</i>	Cyclops acacia	ex	0	0	0	0.5%	0	0
<i>Eucalyptus globulus</i>	Blue gum	ex	0	0	0.1	0.3%	0	0.3%
<i>Schinus terebinthifolius</i>	Brazilian pepper tree	ex	0	0	0	0.3%	0	0.3%
<i>Salix laevigata</i>	Red willow	N	0	0	0	0.3%	1%	0
<i>Tamarix aphylla</i>	Athel	ex	0	0	0	0.3%	0	0
<i>Artemisia douglasiana</i>	Mugwort	N	0	0	0	0.3%	0	0
<i>Sambucus nigra</i> subsp. <i>canadensis</i>	Blue elderberry	N	0	0	0	0.3%	0	0
<i>Malosma laurina</i>	Laurel sumac	N	0	0	0	0.3%	0	0
<i>Populus fremontii</i>	Fremont cottonwood	N	0	0	0	0	0	0.3%
<i>Morus alba</i>	White mulberry	ex	0	0	0	0	0	0.3%
<i>Foeniculum vulgare</i>	Fennel	ex	0.3	0	0	0	0	0
<i>Schinus molle</i>	Peruvian pepper tree	ex	0.1	0	0	0	0	0
Total number of individuals			57	66	97	396	396	396
Mean number of individuals per quadrat			4.8	5.5	8.1			
SE			0.9	1.3	1.1			

riparian community dominated by three species that exhibit down-slope zonation. Quadrat surveys at 12 sites showed that BASA, SALA, and SAGO had peak densities in different zones: BASA in the High zone (mean of 3 individuals per 100 m²), SALA in the Intermediate zone (3.4 individuals per 100 m²), and SAGO in the Low zone (5.9 individuals per 100 m², Table 1). Line-surveys at the same 12 sites showed that, of the 25 perennial shrub and tree species present, BASA, SALA, and SAGO accounted for a high percentage of the individuals overall (88%), and each had its greatest relative abundance in a different zone: BASA accounted for 68% of individuals in the High zone; SALA for 78% in the Intermediate zone; and SAGO for 76% in the Low zone (Table 1). Zonation of BASA, SALA, and SAGO was seen at all 12 survey sites, and the pattern was significant within each site (G-test, df = 4, P < 0.001) and for the valley as a whole (pooled data, G-test, n = 1041 individuals, G = 1254, df = 4, P < 0.001). There was relatively little overlap between the adult distributions of the three species: on average, BASA and SALA had 17% overlap ($\pm 0.3\%$ SE); BASA and SAGO

had 7% overlap ($\pm 0.3\%$ SE); and SALA and SAGO had 22% overlap ($\pm 0.2\%$ SE; n = 12).

Distribution of Seedlings

The seedling profile at one site showed that new BASA, SALA, and SAGO recruits established in high numbers, up to 3375 seedlings per m² (Fig. 3). BASA seedlings were the most broadly distributed and occurred in all zones, with greatest densities in the Intermediate and Low zones. SALA and SAGO seedlings were more narrowly distributed and non-overlapping, with SALA higher on the bank than SAGO. The more extensive surveys at the three recruitment sites also showed that new recruits established in high numbers—up to an average of 1523 seedlings per m² (Low zone at New Channel)—and exhibited the same distribution patterns (Table 2). At all three sites, BASA seedlings had relatively high densities in all zones, SALA seedlings occurred almost exclusively in the High and Intermediate zones, and SAGO seedlings occurred almost exclusively in the Low zone.

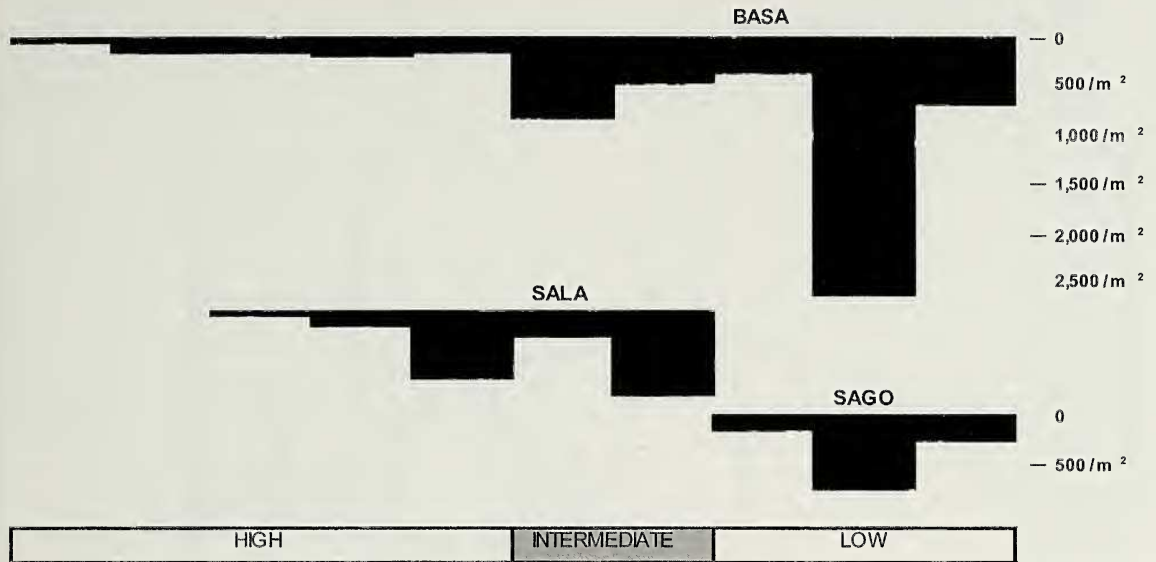


FIG. 3. A profile of the seedlings at a recruitment site in the Tijuana River Valley. Seedling densities are shown as number per m^2 . The profile was done on a steep bank, and the transect was 6 m long.

Among seedlings, therefore, SALA and SAGO exhibited clear zonation but BASA did not. Zonation of SALA and SAGO seedlings was significant within each site (G -test, $df = 2$, $P < 0.001$) and in the pooled total for the three sites (G -test, $n = 3411$ individuals, $G = 3755$, $df = 2$, $P < 0.001$). The distributions of SALA and

SAGO seedlings were so distinct that they overlapped by only 3%, 9%, and 17% at the three sites. In contrast, the distribution of BASA seedlings overlapped extensively with both SALA (55%, 44%, and 49%) and SAGO (33%, 65%, and 68%) in the three sites.

SALA and SAGO seedlings exhibited zonation similar to that observed among adults (SALA higher on the bank than SAGO, with little overlap in their distributions). In contrast, BASA seedlings were far more broadly distributed than adults, and they were most dense in the lower zones where BASA adults were virtually absent.

TABLE 2. SEEDLING DENSITY IN THE HIGH, INTERMEDIATE, AND LOW ZONES AT THE THREE RECRUITMENT SITES IN EARLY SUMMER 2010. Numbers are means per m^2 ; n = number of quadrats. BASA = *Baccharis salicifolia*, SALA = *Salix lasirolepis*, and SAGO = *Salix goodingii*.

Recruitment site	HIGH	INT.	LOW
NEW CHANNEL			
BASA	407	840	1287
SALA	330	518	1
SAGO	0	48	236
TOT	737	1406	1523
SE	136	140	157
n	21	30	35
DIRT ROAD			
BASA	539	1078	694
SALA	780	368	1
SAGO	0	13	396
TOT	1319	1460	1091
SE	230	377	175
n	33	15	39
DAIRY MART			
BASA	11	10	27
SALA	49	23	0
SAGO	4	7	110
TOT	64	40	137
SE	12	8	23
n	27	31	30

Factors Affecting Recruitment

Fruiting phenology. The three species had different fruiting curves (Fig. 4). BASA produced seeds during the entire study period (December 2009 to August 2010), and 95% of its seeds were produced in the six months between January 6 to July 14. In contrast, SALA and SAGO produced seeds for short periods during spring. SALA fruited first with a peak in mid-March, and 95% of its seeds were produced in the 10 weeks from February 24 to April 28. SAGO fruited later with a peak in mid-May, and 95% of its seeds were produced in the 13 weeks from April 21 to July 14. Peak seed production in SALA and SAGO was nine weeks apart, and there was only a 7.4% overlap in their seed production curves.

Timing of recruitment. Seedlings of the three species were abundant in the recruitment pots, with total mean densities up to 136 seedlings per pot (7667 seedlings per m^2). The three species had different recruitment curves (Fig. 5). BASA

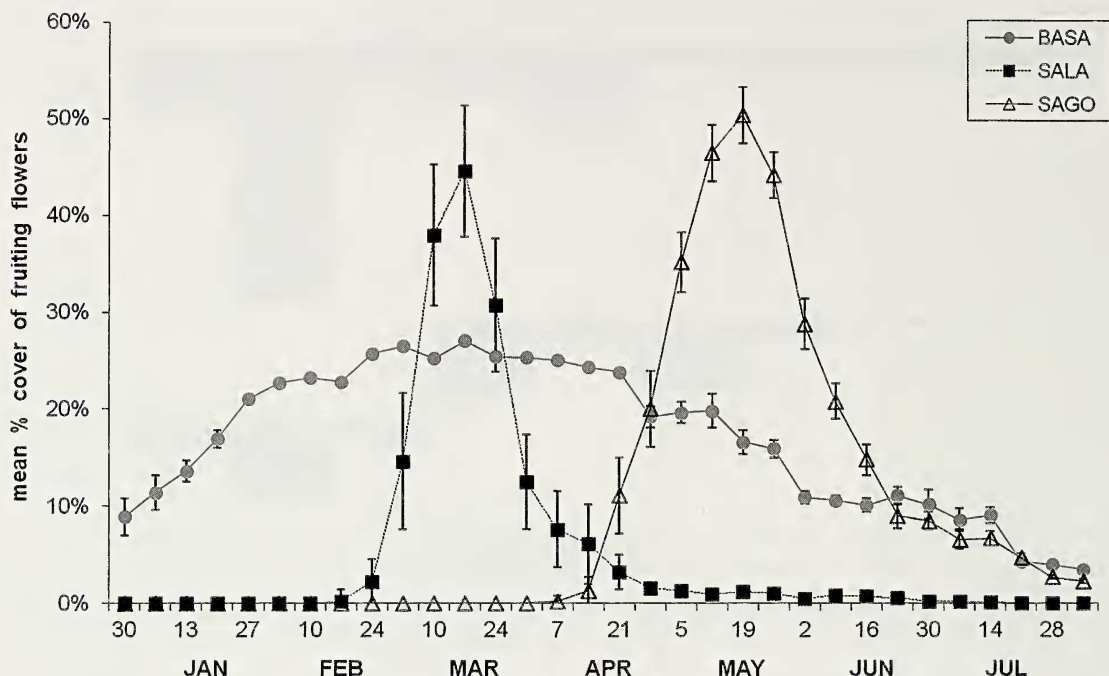


FIG. 4. Fruiting periods of BASA, SALA, and SAGO during 2010. Data are means ± 1 SD.

recruited over a broad period from January through June. In contrast, SALA and SAGO recruited for shorter periods. SALA recruited from February to April, with a peak in March. SAGO recruited from April to June, with a peak in May. Peak recruitment in SALA and SAGO

were eight weeks apart, and there was only a 1% overlap in their recruitment curves.

For all three species, the number of seedlings in the pots during a given month was positively correlated with the intensity of fruiting of the adults during that month. The correlations were

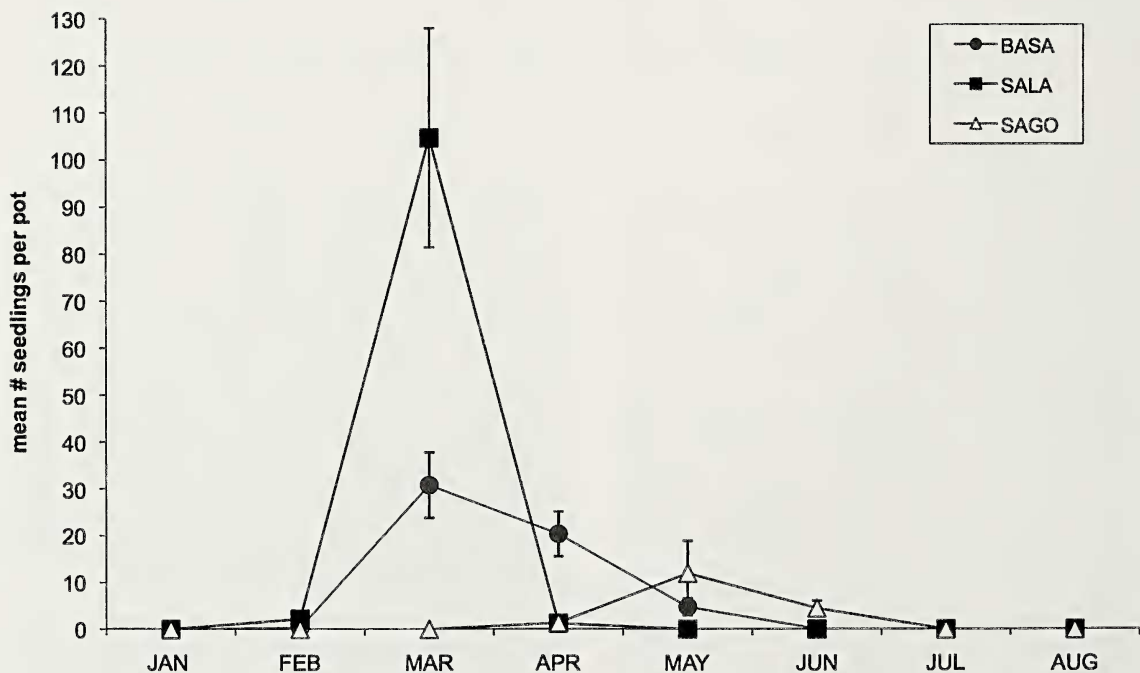


FIG. 5. Density of BASA, SALA, and SAGO seedlings in recruitment pots during 2010. Error bars are ± 1 SE ($n = 2$ sites). Density per pot can be converted to density per m^2 by multiplying by 55.6.

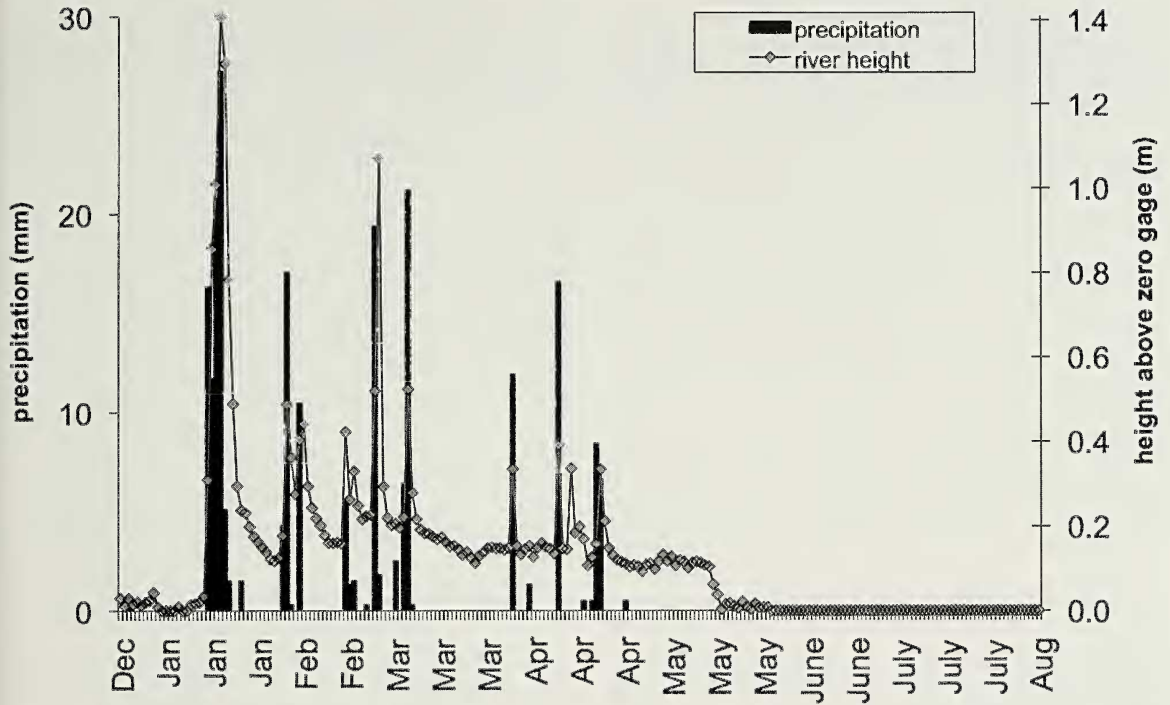


FIG. 6. Daily precipitation and river height in the Tijuana River Valley for December 28, 2009 to August 5, 2010. Data cover the period during which fruiting and recruitment were studied.

relatively weak and not significant for BASA ($r^2 = 0.496$; $P = 0.05$). The correlations were strong and significant for SALA ($r^2 = 0.976$; $P < 0.001$) and SAGO ($r^2 = 0.913$; $P < 0.001$) and for the total community ($r^2 = 0.535$; $P < 0.05$). These results indicate that there was close coupling between the timing of fruiting and the timing of recruitment.

Water-level change and the predicted distribution of seedlings. Water levels in the Tijuana River Valley fluctuated with rainfall during the study period (Fig. 6). They reached their highest levels (1.4 m) during January when rainfall was heavy and dropped to zero during May. The Seedling Distribution Prediction Index, based on fruiting and water-levels, predicted that: (1) SALA and SAGO seedlings would have nearly non-overlapping distributions (only 5% overlap); (2) SALA seedlings would be higher on the bank than SAGO seedlings; and (3) BASA seedlings would occur within all zones and overlap extensively with SALA and SAGO (overlaps of 48% and 36%, respectively). These predictions were all consistent with the observed seedling distributions.

Post-recruitment Factors

Seedling survivorship. During the first summer, seedlings of all three species survived well in all zones, with the exception of SALA seedlings in

the High zone (Table 3); summer survivorship for SALA in the High was only 3%, in contrast to 41% for BASA, which was also abundant in that zone. Many young SALA seedlings (<10 cm tall) were standing dead in the High zone during summer 2010, and they appeared to have died from desiccation. The result was that SALA densities in the High zone declined from an initial average of 386 seedlings per m^2 to an average of only 12 individuals per m^2 at the end of summer.

During the first winter, seedlings of all three species survived well in most zones except for BASA seedlings in the Low zone (Table 3); winter survivorship of BASA in the Low was only 0.2%, in contrast to 19% for SAGO, which was also abundant in that zone. Many BASA yearlings (1.1–1.9 m tall) were standing dead in the Low zone during early spring 2011. They were in pools of shallow water and appeared to have died from sustained anoxic conditions around their roots. In addition, many BASA yearlings could not be found and appeared to have been washed away by the winter flows. The result was that BASA densities in the Low zone declined from an initial average of 608 seedlings per m^2 in late summer to an average of only 1 individual per m^2 by the end of the first winter.

Overall, despite many deaths during the first year, yearlings of the three species had total average densities of 22–59 per m^2 and formed dense, green thickets 1.0–2.5 m tall in all zones. The yearlings also displayed a zonation that was

TABLE 3. SEEDLING DENSITY AND SURVIVORSHIP IN THE HIGH, INTERMEDIATE, AND LOW ZONES. 3A. Seedling density censused at three times; numbers are means per m² (n = 3 sites). 3B. Seedling survivorship (%) calculated from the densities in A. An 'x' indicates that initial densities were too low to measure survivorship (<2 individuals per m²). BASA = *Baccharis salicifolia*, SALA = *Salix lasiolepis*, and SAGO = *Salix gooddingii*.

		HIGH	INT.	LOW
A. DENSITY				
1. Early summer 2010	BASA	319	643	669
	SALA	386	303	1
	SAGO	1	23	247
2. Late summer 2010	BASA	130	490	608
	SALA	12	226	1
	SAGO	1	8	106
3. Early summer 2011	BASA	21	16	1
	SALA	3	41	1
	SAGO	0	2	20
B. SURVIVORSHIP				
After first summer (A1 to A2)	BASA	41%	76%	91%
	SALA	3%	75%	x
	SAGO	x	33%	43%
After first winter (A2 to A3)	BASA	16%	3%	0.20%
	SALA	28%	18%	x
	SAGO	x	21%	19%

similar to the adult zonation pattern, except that BASA yearlings were still abundant in the Intermediate zone.

Riparian woodland development. To determine how and when BASA was essentially eliminated from the Intermediate zone, several aspects of the developing community were examined (Table 4). **Plant densities** decreased with age in all three zones. Densities were high at the time of recruitment (707–969 individuals per m² on average) and were four orders of magnitude lower in the 19-year-old stands (0.06–0.11 individuals per m² on average). **Canopy heights** increased with age in all three zones. The greatest canopy heights were in the Low zone of 19-year-old forests, where trees reached an average height of approximately 12 m. **Canopy cover** increased with age in the Intermediate and Low zones where it was almost 100% in 7- and 19-year-old stands; it remained 4% or less in the High zone. **Light levels** decreased with age in the Intermediate and Low zones, to less than 15% in 7- and 19-year-old stands; they remained 100% in the High zone. Overall, the community structure changed rapidly with age. In the Intermediate and Low zones, a dense forest grew up with a tall and dense canopy that greatly decreased the light levels within.

BASA skeletons. In the Intermediate zone of 19-year-old woodlands, the maximum height of dead BASA individuals averaged 3.3 m (± 0.6 SD; n = 40), whereas the height of the overhead SALA canopy averaged 8.3 m (± 1.1 SD; n = 40). The presence of full-grown but dead BASA indicates that conditions in the Intermediate zone were initially favorable for growth, but condi-

tions deteriorated some time after BASA had reached adult size.

DISCUSSION

This study of a riparian woodland in southern California demonstrated that BASA, SALA, and SAGO were numerically and structurally dominant, and that they displayed a significant down-slope zonation pattern not previously described. Investigation of seed production, seedling recruitment, seedling survivorship, and community development identified the factors most responsible for the adult zonation patterns, and showed that the factors for SALA and SAGO were different than those for BASA.

Factors Affecting Recruitment

The zonation of SALA and SAGO was established at the time of recruitment, and the factors most responsible were the timing of fruiting and the timing of water-level changes. Seeds of these species germinated in the moist sediment just above the water line, and the two species established in sequence on the bank as the water level dropped. SALA established higher on the bank because its seeds were dispersed earlier when water levels were higher; SAGO established lower because its seeds were dispersed later when water levels were lower. The fruiting periods of SALA and SAGO were separate enough, and the water-level decline was steady enough, to result in distinct zonation of the seedlings. This zonation pattern observed among seedlings was retained as the stand aged and observed among adults (with only minor post-recruitment modification). Because

TABLE 4. CHARACTERISTICS OF RIPARIAN WOODLANDS IN THE TIJUANA RIVER VALLEY. Numbers are means (and SE) for density, canopy height, canopy cover, and light level in the High, Intermediate (INT), and Low zones of stands of four ages.

	HIGH				INT				LOW			
	0.5	1.5	7	19	0.5	1.5	7	19	0.5	1.5	7	19
STAND AGE (yrs)												
DENSITY (#/m ²)	707 (363)	24 (9)	2.3 (0.1)	0.06 (0.01)	969 (465)	59 (26)	1.3 (0.1)	0.08 (0.02)	917 (410)	22 (4)	1.4 (1.0)	0.11 (0.02)
CANOPY HEIGHT (m)	0.3 (0.0)	1.7 (0.4)	1.8 (0.1)	3.0 (0.2)	0.2 (0.1)	1.9 (0.2)	6.6 (0.3)	9.0 (0.2)	0.1 (0.0)	1.6 (0.4)	7.7 (1.2)	11.8 (0.5)
CANOPY COVER (%)	0 (0)	0 (0)	4 (3)	0 (0)	0 (0)	0 (0)	97 (3)	98 (1)	0 (0)	0 (0)	96 (1)	97 (1)
LIGHT (% of ambient)	100 (0)	100 (0)	100 (0)	100 (0)	100 (0)	100 (0)	15 (8)	9 (2)	100 (0)	100 (0)	9 (2)	9 (2)

factors that affect recruitment play a primary role in their adult distributions, SALA and SAGO provide a new example of the supply-side influencing zonation in a community (Grosberg and Levitan 1992; Sousa et al. 2007).

The combination of fruiting period and water-level change as factors influencing seedling distribution has been predicted elsewhere for other species, usually with the proviso that sediment grain size and moisture content of the soil also play important roles (McBride and Strahan 1984b; Niiyama 1990; Van Splunder et al. 1995; Mahoney and Rood 1998). However, the recruitment pots used in this study eliminated these physical factors as alternative explanations for the observed zonation of seedlings, because the pots always contained the same sediment grain size and soil-moisture content. In addition, the Seedling Distribution Prediction Index based only on fruiting and water-levels predicted the observed zonation of the seedlings.

It is unusual for fruiting period to play an important role in the structure of any community (Levine and Murrell 2003; Morissette et al. 2009), but the willow-dominated, riparian forest in this study has three characteristics that allow fruiting period to play such a role. First, events from fruiting to seedling recruitment occurred quickly with no time lags. It takes just minutes for wind-blown seeds to disperse to recruitment sites and, when the seeds land in a suitable area, they germinate within a few hours (Emery 1988; Young and Young 1992; Karrenberg et al. 2002, Boland, unpublished data). Fruiting period is unlikely to play an important role in community structure if species have persistent seed banks, longer seed-dormancy requirements, or slower dispersal mechanisms. Second, there was a relatively steady shift of recruitment safe sites down the bank as water levels declined. This allowed currently fruiting species to establish in sequence as water levels declined. Fruiting period is unlikely to play an important role in community structure when water-level declines are not orderly. For example, Van Splunder et al. (1995), working on the River Waal in the Netherlands, noted the sequential seed production of four Salicaceae species, but found no clear patterns in the distribution of seedlings because water levels rose and fell several times during seed production. Third, zonation patterns established in the first year were not disrupted by recruitment in later years. Once seedlings established in a disturbed site, they developed into a dense stand of even-aged adults; recruitment in later years, with different water levels and zones of recruitment, was so unsuccessful that it did not modify the zonation patterns of the stand (Boland unpublished data). Awareness of the importance of fruiting period to the distribution of riparian species should improve our general understand-

ing of the role of phenology in species distributions (Chuine 2010).

It has been hypothesized that the early flowering of some wind-pollinated, deciduous trees has evolved because pollination rates are higher when the leaves are not fully developed, and the flowers are more exposed to breezes (Willson 1983). The findings of this study suggest that, for plants like SALA and SAGO, it is more likely that the timing of flowering and fruiting has evolved in response to selective pressure on the placement of seeds at an elevation on the banks where adults are most successful.

Post-recruitment Factors

The adult zonation pattern of BASA is primarily the result of post-recruitment factors affecting survivorship. BASA's long fruiting period translated into a broad vertical distribution of seedlings on the river bank, and post-recruitment mortality narrowed its distribution such that adults were abundant in only the High zone. This study identified two occasions in the development of the community when BASA deaths affected its zonation. During the first winter, nearly all of the BASA that had recruited to the Low zone died. Their deaths were due, in part, to their inability to withstand high flows and, in part, to their inability to survive several months in standing water. BASA, unlike the willows, is not noted for its ability to tolerate fast flows or anoxic conditions associated with standing water (Karrenberg et al. 2002). Then, during the next several years as the forests developed around them, many BASA adults in the Intermediate zone died. As shown by the presence of adult BASA skeletons under the dense willow canopy, BASA adults initially grew well in this zone until they were shaded and outcompeted by the taller-growing willows. Together, these results show that physiological tolerances and interspecific competition are the post-recruitment factors most responsible for the adult zonation of BASA. Because post-recruitment factors play the primary role, BASA is a new example of the interaction side (Roughgarden 2009) determining zonation in a community. BASA also appears to be an example of a competitively inferior plant that is forced to inhabit a more stressful zone (Grime 1979; Pennings and Bertness 2001).

This study has shown that the positions of the zones and the main zonation patterns observed among adults are established by the end of the first year. At that time, the Low is dominated by SAGO, the Intermediate by SALA (and BASA), and the High by BASA. During later development the configuration of the bank may be altered through erosion or sedimentation, but the zones stay in essentially the same place. After 20

or 30 yr the cohort of initial recruits has developed into even-aged stands in each zone.

The overall goal of studying patterns in this riparian woodland was to gain an understanding of the processes important in shaping the community. The study found that several factors acted consecutively to produce the species' zonation; fruiting period and water levels acted first to produce seedling patterns, which, in SALA and SAGO, were retained to adulthood. Then physiological tolerances and interspecific competition acted to modify the seedling pattern, especially in BASA. The simultaneous study of seed production, recruitment, seedling survivorship, and woodland development showed where and when factors were important for each of the dominant species in the community.

Applications in Riparian Restoration Projects

The results of this study provide much-needed information to help managers plan and conduct riparian restoration projects in southern California. The two basic approaches to riparian restoration are horticultural restoration (Griggs 2009) and natural restoration (Briggs 1996). In southern California, horticultural restoration is typically used; nursery-grown container plants are planted in low densities, and farming practices, such as irrigation and weed control, are used to sustain the plants for the required maintenance period, usually five years (Griggs 2009). This is the appropriate method in sites that are not inundated by winter floods and at sites that are distant from a natural seed source. However, horticultural restoration can be costly and is not always successful; often there are extensive deaths when the irrigation is discontinued, and often the installed assemblage does not resemble a natural riparian community (Boland personal observation).

This study can provide some guidance for horticultural restoration projects regarding species relative abundances, spatial arrangements, and densities. First, because this study found that only a few species are dominant among the many present, horticultural projects should use a species palette that approximates these unequal natural relative abundances. Second, because this study showed a down-slope zonation of the dominant species, horticultural projects should plant species clumped in the appropriate zones as opposed to random, haphazard, or other mixed arrangements. Finally, because this study showed that 19–32-year-old natural riparian woodlands are relatively dense, horticultural projects should plant at high densities. If, for example, one assumes a 95% annual survivorship rate over 19 years for installed plants, then initial planting densities would need to be 2.6–4.4× greater than typically used at present (~200 per acre, or ~500

per ha; River Partners 2007) to equal natural, 19-year-old densities. By making the relative abundances, spatial arrangements, and densities more closely resemble those observed in natural riparian communities, restoration projects that use a horticultural approach are more likely to be successful.

The alternative to horticultural restoration is natural restoration. In natural restoration, a site is prepared (usually cleared and graded), and revegetation is allowed to proceed naturally with little or no human intervention (Briggs 1996). This is an appropriate method in sites that are inundated by floods during winter and which have natural seed sources nearby. If properly timed and carried out, this method can be more effective and less costly than horticultural restoration. Unfortunately, natural restoration is rarely used in southern California at present.

This study provides the empirical foundation needed for managers to use the natural restoration approach. In particular, knowing that fruiting period and recruitment are so closely linked means that one can predict *when* the dominant riparian species will recruit. Also, knowing that recruitment safe sites and water level are so closely linked means that one can predict *where* the recruitment will occur. In natural restoration, this time-and-place predictability is of critical importance because success relies on water-level decline coinciding with peak seed production (Mahoney and Rood 1998). If a project involves the breaching of a berm to flood a restoration site, the water-level decline can be timed to ensure the recruitment of desired species to the site.

In rangeland sites, natural restoration (called natural recovery in rangeland literature) has been criticized for slow development, dominance by undesirable plants, unpredictable results, and excessive herbivore damage (Whisenant 1999). Clearly, these problems have not occurred in the natural development of riparian sites of the Tijuana River Valley, where development was rapid, native plants were dominant, and there was little evidence of herbivore damage. In addition, the riparian woodlands that have developed naturally at these sites are of high quality and support many species, including endangered bird species. Natural restoration may be more successful in riparian habitats because, unlike rangelands, riparian communities are well adapted to frequent, extensive disturbances and have the ability to regenerate quickly after a disturbance (Faber et al. 1989; Sher et al. 2002).

Ideally, natural restoration will become more common in southern California in the future because it has several characteristics that make it superior to horticultural restoration. First, it produces a community with a high density (and

cover) of seedlings and adults. If adult riparian trees are nearby (Friedman et al. 1995), recruitment is likely to be on the order of 40–1500 seedlings per m² as observed in this study. Over time, naturally recruited stands will remain denser (and have greater cover) than horticulturally restored stands. In the Tijuana River Valley, densities within 7-year-old stands were 26× greater than—and densities within 19-year-old stands were approximately double—the *initial* planting density of a typical horticultural project (~200 individuals per acre, or ~500 per ha; River Partners 2007). Second, natural restoration produces a community with the appropriate spatial distribution of species, including the down-slope zonation of dominant species. In horticultural restoration projects, species are often mixed in space resulting in poor survivorship of individuals planted at less than optimal elevations, especially once irrigation has been discontinued. Third, natural restoration results in a community in which local plant species have appropriate sex ratios and genetic diversity (Briggs 1996; Landis et al. 2003). Some horticultural practices, such as the use of multiple cuttings from only a few source individuals or use of non-local stock, can result in unnatural sex ratios or unnatural genetic diversity among the installed plants. Finally, natural restoration is likely to be considerably less expensive than horticultural restoration. It requires no container plants or workers to plant them, no irrigation systems or workers to install and maintain them, and no weed control or post-recruitment maintenance.

Because of the substantial benefits of natural restoration of riparian habitats, resource agencies with the authority to approve restoration plans should require that natural restoration be attempted before horticultural restoration at sites where such an approach would be appropriate. Greater emphasis on natural restoration will require a shift in the way restoration projects are planned, approved, and conducted, but likely would lead to decreased costs, increased quality, and improved long-term success of restoration projects.

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